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SOME POINTS IN THE STRUCTURE OF THE ACANTHOCEPHALA

BY H. W. GRAYBILL

WITH ONE PLATE

In the singular group of parasitic worms known as the Acanthocephala, the large nuclei of the subcuticula and lemnisci are most interesting and unique structures. They lie in a mass undivided by cell walls and in the adult worm are usually present in great numbers. Even in the same individual they may present an astonishing number of sizes and forms. In size they vary from moderately small structures to enormously extended bodies, as in the lemnisci of *E. clavula* Duj. (Hamann 91). Their form may be either spherical, ovoid, or amoeboid. These nuclei divide directly, and probably have to some degree the ability to move (Hamann 91, 95). In the living parasite they have been observed to push out and withdraw pseudopodia-like processes (Kaiser 93, p. 29). They are not only found in the substance of the lemnisci and subcuticula but are frequently seen lying in the lacunae of the same.

In the subcuticula and lemnisci of an echinorhynchus collected from the rock bass (*Ambloplites rupestris*) and black bass (*Micropterus dolomieu*) of the Great Lakes are found nuclei of such extraordinary size and form that an extended description of them seems called for.

It will suffice here to say that the subcuticula of this worm is of the ordinary type, being bounded externally by a thin cuticula and internally by a delicate basement membrane (*membrana limitans*). The radical and the peripheral fiber systems are well developed. Near the membrana limitans is located the usual set of canals, consisting of two large lateral vessels extending nearly the whole length of the animal and a meshwork of lacunae connecting the two both dorsally and ventrally. The nuclei referred to above lie approximately in the middle of the subcuticula immediately beneath the innermost layer of peripheral fibers.

A stained mount of the body wall spread out shows, under low magnification, along the middle of both the dorsal and the ventral sides, a deeply stained, well-formed, dendritic mass (fig. 12), which appears at first sight to extend continuously almost from one end of the body to the other. On closer examination, especially under a higher power, it is found that each of the supposed single masses is divided into several parts which follow each other more or less closely. A glance shows that these several long branching bodies (nuclei) are independent of the lacunae which lie in a different level and form a complete network between the lateral canals.

Each nucleus consists of a more or less sinuous main trunk, which lies about midway between the two lateral canals. It is not uniform in width, but is successively contracted and expanded, having a maximum width of 14 μ. On either side are given off, about at right angles, a large number of branches which may be simple or variously branched. The branches usually come from the nodes of the main trunk. They are at times moderately uniform in width, while again they may be contracted at one or more places to a minute fiber. In fact, under low magnification, many small roundish or irregularly shaped portions of nuclear matter appear to be disconnected from the surrounding branches. However, under a high power it is found, in all but a very few cases, that a drawn-out thread of nuclear matter definitely connects each of these to a near-lying branch. Some of the few truly isolated portions had certainly separated from the main mass just previous to or at the time of killing, as a drawn-out point of nuclear matter from the isolated part pointed directly toward a similar projection on a neighboring branch.

The width of these branching nuclei is such that they occupy approximately the middle half of the spaces between the lateral canals. In some cases, however, the branches approach quite close to these canals, especially when the ends of two successive nuclei pass each other somewhat (fig. 12).

The various branches of the nuclei are so arranged with respect to the net-work of lacunae that they occupy as much as possible median positions in the islands of hypodermis between the lacunae.

The number of dendritic nuclei in the body varies from about ten to twelve. In length they vary in good sized worms from 2 to 4.6 mm. They stop short some distance from the anterior and posterior ends of the body, so that in sections from these regions no nuclear matter is encountered.

In each lemniscus is found a single large nucleus. The lemnisci are very long, thread-like bodies. Each is divided into two moderately distinct regions; a proximal, broader, flat region, 450 to 900 μ long, and a distal cylindrical region many times longer than the former. The large nucleus is located in the proximal portion of each organ. It is, roughly speaking, of a branching type and in length occupies nearly the whole of this region of the lemniscus. In sections its outline is usually dentate or irregular (fig. 10).

Each nucleus is formed of a longitudinal portion of very ununiform width with a maximum of 56 μ. Attached along the sides of this are a few short branches which are in some cases expanded at their ends into broad masses.

The lacunae of both regions of the lemnisci are frequently filled with a granular coagulum which at most stains very lightly.

It is interesting to note here that Hamann (91, p. 146) found only a single nucleus in each lemniscus of *E. clavula* Duj. The measurements given by him for this nucleus are, length 1.6 mm., breadth 0.15 mm. However, the nuclei of the subcuticula were of the usual type and showed well the various division stages. (The writer is very greatly indebted to Dr. Otto Hamann of Berlin for slides of this, as well as of various other species, which he so kindly forwarded at the request of Dr. H. B. Ward.)

The nuclear substance of the above described branching bodies stains very uniformly. Only under the highest power is it found to be compactly granular in structure. It contains a moderate number of vacuoles of various sizes which usually are bounded by definite circular outlines (figs. 3, 5, 7, 10).

Chromatic bodies or nucleoli are present in the nuclear substance in countless numbers. In form they vary greatly, being spherical, ovoid, irregular, or long and thread-like. Those of the first three types predominate. They vary in size from the minutest granules to structures 22 μ long. Those filamentous in form, though only about 1.5 to 3 μ in width, may, in exceptional instances, reach a length of 84 μ. They are not always uniform in width throughout. Frequently they are very weakly expanded and contracted at intervals along their whole length. In some cases this is so pronounced as to give a distinctly moniliform appearance to the chromatic body.

In fig. 9 are represented some of the irregular forms of the above chromatic bodies. The remaining figures will readily give an idea of other forms. They stain very deeply. They may contain one or several small roundish transparent specks which are probably vacuoles. Even after the stain has almost entirely washed out of the nuclear matter no structure is to be detected in these chromatic bodies which are still quite deeply stained.

At times in the nuclei of the lemnisci the roundish chromatic bodies occur in groups, and in some cases they lie in contact, forming rather compact masses.

In general the larger chromatic bodies and frequently also the smaller ones are surrounded by unstained halos which have usually a distinct boundary, the same as the vacuoles spoken of above (figs. 1–8). These halos are not so frequent in the nuclei of the lemnisci. Hamann (91) describes and figures similar halos in a nucleus from a lemniscus of *E. clavula* Duj.

Some of these chromatic masses are suspended in the halos by minute chromatic strands which radiate from them, connecting with the nuclear substance (figs. 1 and 2).

In cross-section the different branches and the trunks of the branching nuclei are circular, oval, or oblong. And since in sagittal sections of the body, especially just to one or the other side of the main trunks of these nuclei, most of the branches are shown in cross-section, an appearance of the subcuticula is presented not unlike that found in echinorhynchi where the nuclei are comparatively small in size and large in numbers. The extensive branching brings portions of these dendritic nuclei into most of the regions of subcuticula, and also gives to them an enormous surface area for the carrying on of metabolic processes.

In another species of echinorhynchus (host—*Moxostoma* sp.) which is related to *E. proteus* West, among the many spherical, ovoid, and amoeboid nuclei of the subcuticula were also found a few very large ones which were dendritic in form. The longest one measured had a length of 630 μ. Some of the medium sized ones of this type possessed as many as seven good sized branches.

A comparison of the branching nuclei in the first form considered above, with the nuclei in *Neorhynchus clavaeceps* (Zed.), and *N. agilis* (Rud.) is interesting. According to Hamann these two forms represent sexually mature larvae. Each possesses six to ten large (0.2 mm.) ovoid nuclei in the subcuticula of the body and two in each lemniscus. In the form studied the number of nuclei is also small, there being ten to twelve in the body and one in each lemniscus. As suggested above, the branching is probably both for the purpose of increasing the superficial area and bringing portions of the nuclei into all regions of the subcuticula. The total amount of nuclear matter is immeasurably greater than that contained in the few ovoid nuclei of *N. agilis* and *N. clavaeceps* and is probably about the same as in cases where the subcuticula contains large numbers of small nuclei.

In the development of the nuclei of the subcuticula in the echinorhynchi as worked out by Hamann (91) and Kaiser (93) one may distinguish roughly three stages. In the first stage the nuclei are large, roundish bodies and few in number. In the second stage the number of nuclei is still small, but their form is amoeboid with pseudopodia-like processes extending out from the various sides. The third stage is characterized by a large number of small nuclei of various sizes and forms and is brought about by an extensive fragmentation of the amoeboid nuclei of the previous stage. However, though this is the usual mode of development, Hamann has pointed out in the case of *N. clavaeceps* and *N. agilis,* forms already referred to, that in the adult the nuclei have remained at the first stage of development.

In view of this development it therefore seems probable that the above described dendritic nuclei have arisen by an extensive growth of the few large amoeboid nuclei of the larva and that they occupy an intermediate position between the nuclei of the two forms last mentioned above and the nuclei of other forms where they are present in great numbers.

EXPERIMENTS ON THE LEMNISCI.—As stated above, the lemnisci of the echinorhynchus collected from the rock bass and the black bass are very long, thread-like organs. In some cases they reach posterior to the middle of the body. They are unattached except at their points of origin. No muscular layer is present. The single large canal of the posterior or distal portion of the lemniscus divides into two canals on entering the proximal region. These latter canals unite at the attached end of the organ and empty as one canal into the circular canal at the base of the neck. The latter canal connects with the lacunae of the neck and is separated from those of the body by a cuticular ring.

Some experiments were made on living material to determine what effect the cutting off of these well-developed organs would have on the extrusion of the proboscis.

The first experiments consisted in cutting the worm in two immediately posterior to the proboscis sheath, thus severing both lemnisci. A turbid fluid issued from the cut ends of the latter. While in many cases, because of the great injury to the parasite, no motion of the proboscis took place, yet in some few cases the proboscis was completely extruded a number of times.

In numerous second experiments a slit was made in the body wall a little posterior to the base of the neck. Through this opening the lemnisci were drawn out and cut off close to their points of origin. The injury to the worm was slight. In many cases it was found that immediately or after the lapse of some time the proboscis was completely extruded and withdrawn many times with a rapidity equal to similar movements in uninjured worms.

Also, in observing the movements of the fluid in the lacunae of the neck and proboscis of uninjured worms during the extrusion of the latter, it was found that the streaming anteriad always commenced after the beginning of the extrusion and never preceded it. Again, when extrusion ceased, the fluid of the lacunae for some time continued to stream anteriad and adjust itself as it would not have done if under pressure sufficient to have aided in the extrusion.

From the above observations it seems plain that in this form at least the lemnisci take no part in the protrusion of the proboscis (Hamann 91, p. 150), and also that any pressure on the fluid of the body cavity is not necessary to the operation.

DESCRIPTION OF THE SPECIES.—With the aid of material kindly sent by Dr. E. Linton to Dr. H. B. Ward, for purposes of comparison, the writer was able to determine definitely the identity of the form concerned in this paper with that from *Roccus americanus* described by Linton (92, p. 528) as *Echinorhynchus thecatus.* As the original description is very brief, being based almost entirely on toto mounts of the parasite and on the measurement of only a few individuals, the following more extensive list of the important characters, including measurements of hooks and of a large number of individuals, will be of great systematic value.

Living specimens flattened dorso-ventrally, smooth. Color white, light yellow, orange, or gray. Preserved specimens cylindrical, curved. Proboscis also curved when extruded. Transverse wrinkles only on anterior half of body. Maximum diameter of body in female toward anterior end, in male at or slightly anterior to middle of body. In both sexes gradual decrease in diameter to anterior end where neck joins abruptly. Similar decrease posteriad in case of male. End moderately blunt. In female posterior end slightly expanded, very blunt. Neck increases in diameter to base. Proboscis usually broadest at middle. Anterior end rounded. Hooks, 24 to 31 transverse and 12 longitudinal rows, surrounded by prominent collars. Collars of hooks at the base of the proboscis frequently longer than hooks. Recurved base of hooks notched at end. Lemnisci long and thread-like. Proboscis sheath double-walled. Ganglion in midst of proboscis retractors, midway between anterior end of proboscis and base of sheath. Nuclei of circular muscle layer arranged in two lateral bands, one opposite each lateral canal. Testes contiguous, anterior one the longer. Cement glands in compact mass, eight in number. Embryos spindle-shaped.

MEASUREMENTS

	LENGTH	WIDTH		
		ANTERIOR	MAXIMUM	POSTERIOR
Body, female.	11–26 mm.	0.51–0.89 mm.	0.8–1.4 mm.	0.52–1 mm.
male ..	7–12 mm.	0.39–0.69 mm.	0.59–0.95 mm.	0.37–0.75 mm.
Neck........	179–298 μ.	209–298 μ.	....	254–388 μ.
Proboscis....	868-1164 μ.	....	239–328 μ.	Same as anterior width of neck.
Embryos	85–108 μ.	....	18–22 μ.	....

HOOKS.—In the following table in the case of those hooks of the ventral row with recurved bases, of the two possible measurements of the thorn and the recurved root the longer one is given. The hooks with recurved bases in the dorsal row are measured from corresponding points, just as if the anterior projection were not present. The measurements at the curve were made along the line of maximum width. Values are given in microns.

LONGITUDINAL ROW ON VENTRAL SIDE OF THE PROBOSCIS				LONGITUDINAL ROW ON DORSAL SIDE OF PROBOSCIS		
Transverse row	Length thorn	Length recurved root	Diameter at curve	Length thorn	Length recurved root	
2	72	65	29	65	44	....
4	72	58	29	66	51	....
6	76	69	29	72	40	....
8	76	72	29	72	40	....
10	79	76	32	72	32	....
				Length of hook		Width at base
12	76	76	31	84	....	25
14	72	62	27	79	....	22
16	69	58	22	75	....	20
18	65	27	20	70	....	20
	Length of hook		Width at base			
20	68	....	22	61	....	14
22	68	....	18	61	....	13
26	50	....	14	48	....	13

HOSTS.—*Micropterus dolomieu* and *Ambloplites rupestris;* stomach, pyloric coeca, intestine, and body cavity. *Amia calva* in intestine. Free or attached.

The above work was done in the Zoological Laboratory of the University of Nebraska under the direction of Dr. Henry B. Ward, to whom the writer is under great obligations for many valuable suggestions and for the use of a very extensive collection.

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EXPLANATION OF PLATE

Plate XXVIII

Drawings outlined with camera lucida.

Figs. 1–8. Longitudinal sections of various portions of dendritic nuclei of hypodermis. ×600.

Fig. 9. Variously shaped chromatic bodies found in the same. ×600.

Fig. 10. Longitudinal section of a portion of nucleus in a lemniscus. ×600.

Fig. 11. Hooks of proboscis. ×540.

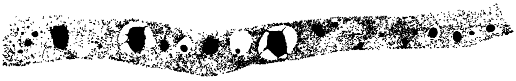
a. Type found on lateral and dorsal (convex) surfaces of anterior half.

b and *e*. Hooks from ventral (concave) surface, anterior portion.

d and *c*. Hooks from posterior portion.

Fig. 12. Microphotograph of flat mount of a portion of the dorsal half of the body wall. Limits of a single nucleus indicated by the arrows. Ends of two adjoining nuclei also shown. Lateral canals and net work of lacunae represented by the light lines.

PLATE XXVIII



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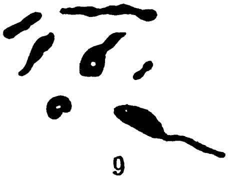

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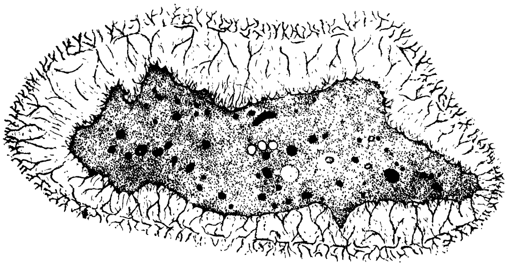

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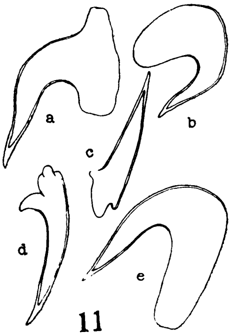

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